Slower than a speeding bullet ant: response to disturbance odor of *Paraponera clavata*

James A. MacIntosh and Michael D. Foote

Abstract: Paraponera clavata, an ant species — commonly known as the giant tropical ant or bullet ant — that inhabits the lowland tropical rainforest at La Selva Biological Station, Costa Rica, belongs to a relatively primitive group of ants that exhibit some social structure but are not eusocial. *P. clavata* emits a strong musk odor in response to aggressive disturbance, and this odor has been proposed to function as an alarm pheromone and/or a warning odor. *P. clavata* is an opportunistic forager with strong mechanical defenses, and therefore has little need for a warning odor. We hypothesized that the musk odor is an alarm pheromone used to recruit other individuals of the same colony. Our results indicate that the odor in fact functions neither as an alarm pheromone nor a warning odor. The use of trail pheromones but not alarm pheromones suggests that the transition between primitive and eusocial ants involves the elaboration of pheromone communication systems.

Key Words: alarm pheromone, giant tropical ant, ponerine ant, warning odor

Introduction

The ponerine ants are a primitive group within the Formicidae that lack the highly structural social system of eusocial ants such as *Atta sp.* (Breed 1985). Breed et al. (1987) suggested that one ponerine species, the giant tropical ant (*Paraponera clavata*), represents an evolutionary transition from independent foraging behavior to the coordinated foraging of many eusocial ants. *P. clavata* emits a recruiting trail pheromone from glands on their ventral side, which are scraped along the ground to attract colony mates to a large food source as the ants return to their nests. (Breed 1985).

Janzen and Carroll (1983) documented another possible pheromone in *P. clavata* by noting that disturbed workers release a strong musk odor, which they hypothesized to be an alarm pheromone and/or a warning odor that functions as an olfactory aposematic. The odor is likely not to have evolved as a warning to other colonies, however, because the colonies are overdispersed and do not patrol their territorial boundaries (Breed et al. 1987). If this overdispersal is caused by colony-specific odor, it is unlikely that ants would only emit the odor when agitated. We observed that though some aggressive interactions took place when an individual was placed near a nest of another colony, the individual was not deterred and sometimes even entered the nest. If the odor functions as a warning during these aggressive interactions, it is puzzling that an intruder would ever enter a foreign nest. Furthermore, *P. clavata* is an opportunistic forager (Janzen 1983) that sometimes kills and feeds on insect prey. It seems unlikely that *P. clavata* would find it necessary or beneficial to deter insects that might be potential prey with a warning odor. *P. clavata* also has a powerful sting and aggressive defense-response that might preclude the need for additional warning defense.

We hypothesized that the musk odor produced during aggressive interactions with *P. clavata* is an alarm pheromone, and not a warning odor. If so, the odor should recruit ants from the same colony from which it was emitted (not ruling out the possibility that the odor might be a general intraspecific attractant that has the same effect on foreign colonies), and the odor should not act as a warning odor by deterring ants from other colonies.

Methods

On the nights of 16 - 19 February 2000, we measured the responses to native and foreign disturbance odors of four haphazardly chosen *P. clavata* colonies in the arboretum of the La Selva Biological Reserve, Costa Rica. Our treatments consisted of exposing each of these four colonies to disturbance-response odors produced by their own colony and by each of the three other colonies. We observed the response of each colony to 20 x 5 cm strips of absorbent paper either left untreated (control), treated with the odor released by their own colony (native colony), or treated with the odor released by one of the other three colonies (foreign colonies). Each strip of paper was observed for 3 min, during which time we recorded the number of ants crossing the paper, the number of ants turning around after making contact with the paper, and the number of ants navigating around the paper after making contact. Additionally, instantaneous counts were taken every 15 sec throughout the observation period to test for possible differences in stalling behavior at the paper.

We first removed ants from their host trees without disturbing the colony (to prevent potential interference from disturbance response of the colony). Four ants from each colony were sealed into a plastic bag, along with 6 strips of treatment paper to hold the musk odor they release in response to disturbance. We recorded ant responses to a strip of control paper taped onto a *P. clavata* foraging trail on the colony's tree and then disturbed a bag of ants by vigorously shaking for 1 min. We immediately removed a strip of paper from the bag, taped it across the foraging trail on the same tree, and recorded ant behavior for another 3 min. On each tree, this process was repeated three times for native colony odor and three times for foreign colony odor (one treatment from each of the three foreign colonies). Trees were left undisturbed for 45 min between each treatment to prevent any cumulative effect of treatments, and control strips of paper were observed before each treatment to control for any differences in baseline ant activity. Latex gloves were worn at all times to inhibit transferal of human scent to any of the experimental papers or trees.

We tested for effects on ant behavior with an ANOVA model that included treatment (control vs. treatment), odor source (native vs. foreign), treatment x odor source, host tree, foreign tree effect (the effect of each foreign tree on the host tree), and time nested within odor source and host tree. Ant behavior was measured with five different source variables: total number of visits, % crossing (crosses / total number of visits), % turning around (turn-arounds / total number of visits), % navigating around (# of ants navigating around / total number of visits), and % stalling (sum of 15-sec instantaneous counts / total number of visits).

Results

The odor released by ants had no significant effect on any of the five measurements of ant behavior either on its own colony or on other colonies (Table 1, Fig. 1). Host trees varied in percent stalling (the ants on tree colony 4 had greater percent stalling behavior than those from the other three colonies, possibly due to colony interference by blocking of their only foraging trail with the paper strips), but none of the other independent variables significantly affected any measures of ant response (Table 1).

Discussion

The musk odor produced by *P. clavata* during aggressive interactions does not appear to be an alarm pheromone in that the odor did not recruit ants from its own colony or any other. Furthermore, it does not appear

Table 1. F-statistics from ANOVAs testing for effects on ant behavior of treatment (control vs. treatment), odor source (native vs. foreign), treatment x odor source interaction, host tree effect, foreign tree effect (the effect of each foreign tree on the host tree), and time nested within odor source and host tree. Ant behavior was measured with five different dependent variables: total number of visits, % crossing (crosses / total number of visits), % turning around (turn-arounds / total number of visits), % navigating around (# of ants navigating around / total number of visits), and % stalling (sum of 15-sec instantaneous counts / total number of visits).

Dependent Variable	Treatment (df = 1,22)	Odor Source (df = 1,22)	Treatment x Odor Source (df = 1,22)	Host Tree (df = 3,22)	Foreign Tree (df = 3,22)	Time [Odor Source, Host Tree] (df = 16,22)
Total Visits	1.06	0.27	0.00	2.64	1.34	0.49
% Crossing	0.12	2.25	3.07	2.04	0.85	0.76
% Turning Around	0.07	0.36	1.81	0.61	0.93	0.47
% Going Around	0.00	0.68	0.00	1.66	1.96	0.80
% Stalling	1.74	0.54	0.17	3.14*	1.48	1.62

*$p \leq 0.05$

to be an olfactory aposematic in that ants from other colonies were not deterred by it. Thus, the musk odor does not seem to function as a pheromone. There are two possible explanations for the lack of pheromone function in *P. clavata:* (1) the ancestors of *P. clavata* may have never possessed an alarm pheromone, or (2) alarm pheromones could have been secondarily lost in *P. clavata,* perhaps due to its powerful self-defense (large body, painful sting, and strong mandibles) and because of energetic or other costs associated with alarm pheromones. Under the latter explanation, the odor that is so obvious to humans may be an evolutionary relic. Future research might locate the gland that produces this musk odor and use strong concentrations of the odor to test for any residual aggressive effects on the ants or for the potential deterrence of larger vertebrate colony intruders.

Although it appears that the odor released in response to disturbance of *P. clavata* is not an alarm pheromone, the rapid response of groups of ants to the disturbance of their colony suggests that the ants have an organized defense response. Perhaps there is an alarm chemical cue that is passed directly from individual to individual, or the mandible clicking that occurs when the ants are disturbed may function as an auditory aposematic. Alternatively, groups of guard ants may be stationed at the colony entrances, ready to attack at any disturbance without need of chemical communication.

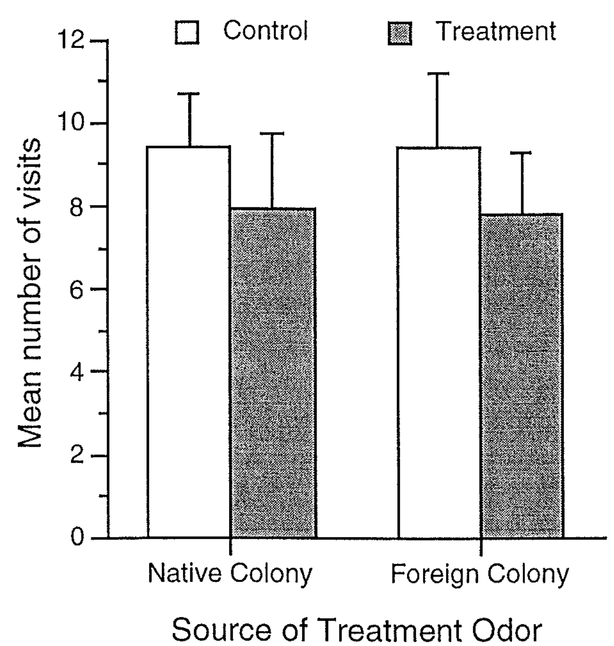

Figure 1. Mean number (± SE) of ants visiting 20 cm x 5 cm strip of paper in 3 min. Strips of paper were left untreated (control) or exposed to the scent emitted in response to disturbance of its native colony or a foreign colony (n = 3 for each bar). The same pattern is apparent for % of ants crossing, turning around, navigating around, and stalling at the experimental paper strips.

It still seems that *P. clavata* represents a transitional stage between primitive nonsocial ants and eusocial ants. They display social organization by employing trail pheromones. Perhaps the odor released in response to disturbance is a precursor to the evolutionary development of alarm pheromones. The capacity to produce olfactory molecules may be a prerequisite for the evolution of pheromone communication systems. Further exploration of olfactory molecules in ponerine ants and other relatively primitive ant groups may shed more light on the evolution of pheromone mediated behavior in social insects.

Literature Cited

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